PERGAMON

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Vision Research 43 (2003) 2905–2914

Vision Research

www.elsevier.com/locate/visres

Effects of light and dark adaptation of rods on specific-hue threshold

Ulf Stabell *, Bjørn Stabell

Department of Psychology, University of Oslo, Box 1094, Blindern, N-0317 Oslo, Norway

Received 10 March 2003; received in revised form 16 July 2003

Abstract

Specific-hue threshold as a function of absolute rod threshold was measured with long-, middle-, and short-wavelength monochromatic test lights presented 17 deg extrafoveally. The measurements were obtained both during the rod phase of long-term dark adaptation and under conditions where the rod receptor system was gradually light adapted from a dark-adapted state by a scotopic background field of increasing retinal illumination. The results show that change in specific-hue threshold with change in absolute rod threshold is not, in general, identical for light and dark adaptation of the rod receptor system. Thus, in the long- and middle-wavelength test regions, the specific-hue threshold could be obtained at higher intensities under the light- as compared to the dark-adaptation condition when absolute rod thresholds were the same. Just the opposite was found for the short-wavelength tests. It is concluded that change in specific-hue threshold with light and dark adaptation of the rod receptor system is not, in general, controlled by the same mechanism.

Keywords: Rod–cone interaction; Colour vision; Light adaptation; Dark adaptation

1. Introduction

It has long been known that saturation of mesopic test colours may be increasingly reduced as the sensitivity of the rod receptor system increases during the rod phase of long-term dark adaptation (e.g., Lie, 1963; Loeser, 1904; Stabell & Stabell, 1965). In a comprehensive study of this relationship, Lie (1963) found that after a strong "white" bleach the intensity level of the specific-hue threshold measured extrafoveally with short- and middle-wavelength tests, first falls rapidly, then remains fairly constant during the cone-plateau period, and lastly, at about the cone–rod break, starts to rise in a negatively accelerated way. Presupposing that the cone mechanisms have reached their absolute dark-adapted states during the cone-plateau period, the rise of the specific-hue threshold during the rod phase of the long-term dark adaptation was explained by the increasing amount of rod signals excited by the test light, reflected in the fall of absolute rod threshold (Lie, 1963).

In contrast to rod dark adaptation, absolute rod threshold rises when the rod system is gradually light adapted by a scotopic background field of increasing retinal illumination (e.g., Stabell & Stabell, 2002). Hence, on the suggestion of Lie (1963), one might expect the specific-hue threshold level to drop with rod light adaptation. Indeed, one might suggest that changes of specific-hue threshold with dark and light adaptation of the rod system are controlled by the same mechanism, that is, by change in amount of rod signals elicited by the test light, reflected in change of absolute rod-threshold level of the test stimulus (see Lie, 1963, p. 476). In the present paper we attempt to test this equivalence hypothesis by measuring specific-hue threshold level as a function of absolute rod threshold both under conditions of rod dark and rod light adaptation. If the hypothesis were valid one would predict that specific-hue threshold as a function of absolute rod threshold of the test light would be identical for dark and light adaptation of the rod system. Thus, when absolute rod thresholds are the same for the light- and dark-adaptation conditions, the specific-hue thresholds should be identical.

Our equivalence hypothesis and prediction are based on the remarkable analysis of Stiles and Crawford (1932, see pp. 194–197). They assumed that "each small patch of the retina is at each instant in a particular state, and that the perceptions there depend only on the light

* Corresponding author. Present address: Eplehagan 10, 1349 Rykkinn, Norway.

E-mail address: kirsten.stabell@epilepsy.no (U. Stabell).

0042-6989/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2003.07.003

incident and on the state of the patch, although many widely different conditions of stimulation of the whole retina may cause the selected area to assume the state in question''. From this basic hypothesis their equivalence principle follows as a necessary consequence: when two different conditions produce the same state in a small retinal area, then any given test light in this area, whatever its nature, will produce the same perception for the two conditions.

The present results show that when the absolute rod thresholds under dark- and light-adaptation conditions are the same, the specific-hue thresholds for a given test light may be markedly different, indicating that the two conditions of adaptation do not produce identical states as defined by Stiles and Crawford (1932). Hence, the results invalidate our equivalence hypothesis.

2. Method

2.1. Apparatus and subjects

The Wright colourimeter and its calibration procedures used in the present study have been described in detail by Wright (1946, see pp. 45–70).

The authors, US and BS, alternately served as observers. Both subjects have normal colour vision as evidenced by normal wavelength discrimination as well as normal responses on Ishihara and Farnsworth–Munsell 100-Hue tests.

An artificial pupil of 2-mm diameter was employed and the light stimulus was directed through the centre of the subject's pupil. By a drum–string device the intensity of the test light could be controlled by the subject, sitting in a light-tight booth, through the operation of a photometer wedge mounted in front of a reflecting prism in the W_2 spectrum. The luminance of the fixation point could be regulated in small steps by the observer so that it appeared just visible during the dark- and light-adaptation periods. The luminance of the ''white'' bleaching field was measured with a Spectra Pritchard 1980A WB photometer, while the radiometric measurements were made with an UDT-370 radiometer. All the observations were made with the right eye and were repeated on four separate occasions to give a mean.

2.2. Experiment I (dark adaptation)

The successive phases of the experiment were as follow:

(1) Dark adaptation 10 min.

(2) The right eye was then exposed for 50 s to a ''white'' (3200 K) uniform bleaching field subtending 30×30 deg, centred 17 deg nasally in the visual field of the right eye. The retinal illumination was 60,000 photopic trolands (ph td).

(3) During the 30 min dark-adaptation period that followed, absolute and then specific-hue thresholds of a 620-nm monochromatic test light of 1×2 deg were repeatedly measured by increasing the test-light intensity in small steps. In order to minimise the effect of the measurements on absolute and specific-hue thresholds, only a few were obtained in each dark adaptation run, and absolute threshold was always measured before specific-hue threshold. Furthermore, in order to control for chromatic adaptation effects, measurements for only one test wavelength were obtained per day. The test field was exposed for 125 ms and it was centred at 17 deg in the nasal field of view of the right eye (same position as the bleaching field). Absolute threshold was obtained when the test light was judged ''just visible'' on two consecutive presentations and specific-hue threshold when two consecutive ''correct'' hue identifications were made.

(4) Phases 1–3 were repeated, except that the wavelength of the monochromatic test light was varied between runs (430, 470, 500, 530, 575, 600, 620, and 650 nm were employed).

A ''correct'' hue identification was obtained when the subject reported a tint of blue (430, 470 nm), green (500, 530 nm), yellow (575 nm), or red (600, 620, and 650 nm).

The use of the criterion ''specific'' (''adequate'' or ''correct'') hue threshold has been discussed by Lie (1963, pp. 423, 428, 434) and this criterion has later been employed by a number of research workers (e.g., Alexander, Fishman, & Derlacki, 1988; Peachey, Alexander, & Derlacki, 1990; Prestrude, Watkins, & Watkins, 1978; Spillmann & Conlon, 1972; Stabell & Stabell, 1965). Yet, since evidence shows that mid-spectral stimuli, in general, appear green when presented steadily, while they often are reported as blue when flashed (Schirillo & Reeves, 2001), one may ask whether the criterion ''green'' has biased the colours of the mid-spectral stimuli upwards. Fortunately, in accord with the observation of Lie (1963, p. 434) no hue was perceived below the correct-hue threshold during the rod phase of the dark-adaptation period under the present conditions of experimentation. For all the test lights the colour changed from a grey-white colour to the hue in question. It should be noted, however, that in order to avoid chromatic adaptation of the cone mechanisms which may produce scotopic contrast hues observable for several minutes (Stabell & Stabell, 1971c), the measurements were well spaced in time and restricted to only a few test flashes during the rod dark-adaptation phase.

Also it should be noted that the non-test eye remained in a completely dark-adapted state under all the experimental conditions of the present study, so that any effect of the non-test eye on the test eye may be assumed to be constant. Previously it has been found that light adaptation of one eye may actually lower the absolute dark-adapted rod threshold of the other eye, although

the effect has been found to be small, only about 0.15-log unit (Reeves, Peachey, & Auerbach, 1986).

2.3. Experiment II (light adaptation)

The successive phases of this experiment were as follow:

(1) Phases 1 and 2 of Experiment I were repeated.

(2) Dark adaptation for about 30 min.

(3) Thereafter the absolute and specific-hue threshold measurements were repeated, except that the 1×2-deg test field was centred on a continuously exposed scotopic background light-adaptation field of 7 deg. The retinal illumination of the background field, illuminated by a monochromatic light of 500 nm, was gradually increased between runs in 1-log unit steps from −3 to 0 log scot td. (The highest background intensity level of 0 log scot td is about 0.3-log unit below the cone-plateau level measured for the 7 deg, 500-nm background light at 17 deg extrafoveally.) The threshold measurements started after 15 s of light adaptation and a threshold response was obtained about 10 s later. About 3 min passed between different runs. Only wavelengths 430–620 nm were employed.

To clarify the mechanisms underlying the change in specific-hue threshold level obtained in Experiments I and II, three supplementary experiments were performed:

Experiment III (dark adaptation; test superimposed on background field): This experiment was a repetition of Experiment I, except that only the 650-nm test light was employed and the 650-nm test light was superimposed on the scotopic background light of 7 deg with intensity held constant at 0.4-log unit below its cone-plateau level.

Experiment IV (dark adaptation; scotopic light added to 650-nm test light): This experiment was a repetition of Experiment I, except that the test light was a mixture of the 650-nm and a 500-nm scotopic light. The intensity of the 500 nm, 1×2 deg scotopic component was held constant at 1.8-log unit below its cone-plateau level, while the intensity of the 650-nm light was increased in small steps to obtain the specific-hue threshold.

At variance with the results obtained during dark adaptation, a blue colour was observed below the "correct" green colours of the 500 and 530-nm test lights under the light-adaptation condition. In Experiment V we tested whether this blue colour response was determined by rod signals of the test light.

Experiment V (light adaptation; threshold of blue with variation of test wavelength): This experiment was a repetition of Experiment II, except that 430, 470, 500, 530, and 550 nm test wavelengths were employed, and the threshold for blue colour was measured. (Note that the criterion "correct" hue identification is not used in this experiment.) The retinal illumination of the background light was held constant at −1 log scot td.

3. Results

The results of Experiments I and II are presented in Figs. 1–7 and show changes in absolute and specific-hue thresholds of the different test wavelengths (430, 470, 500, 530, 575, 600, and 620 nm) obtained both during long-term dark adaptation (section a), and under conditions where the rod receptor system is gradually light adapted from a dark-adapted state (section b). Section c shows the specific-hue threshold levels of sections a and b when absolute rod thresholds are the same for the two conditions. The data points represent the means of four measurements obtained in different runs for subject US, being essentially the same for subject BS. The standard deviation of the four measurements of the absolute and specific-hue thresholds obtained both during dark and light adaptation was about 0.1-log unit.

Fig. 1a illustrates the changes in the absolute and specific-hue thresholds of the 620-nm test light obtained during the long-term dark adaptation. As can be seen, the specific-hue threshold starts to rise steeply at about the cone–rod break of the dark adaptation curve and

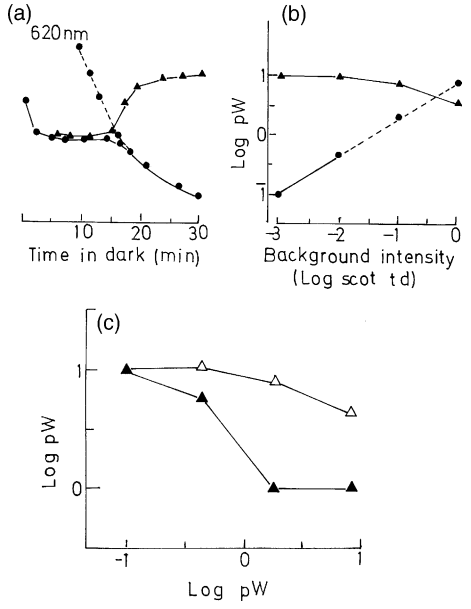

Fig. 1. (a, b) Absolute (●) and specific-hue (▲) thresholds of the 620-nm test light obtained at 17 deg extrafoveally during long-term dark adaptation (a), and with light adaptation of the rod receptor system (b). The stippled curves in this and the following figure represent absolute rod thresholds measured during rod dark and rod light adaptation with the 500-nm test light. (c) shows specific-hue thresholds for dark (▲) and light (△) adaptation of the rod system (ordinate) as a function of absolute rod threshold (abscissa), expressed in log picowatt (10^{-12} W).

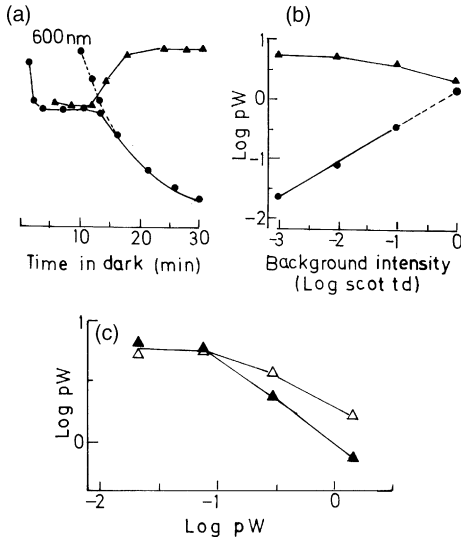

Fig. 2. Same as Fig. 1, except that the 600-nm test light was used.

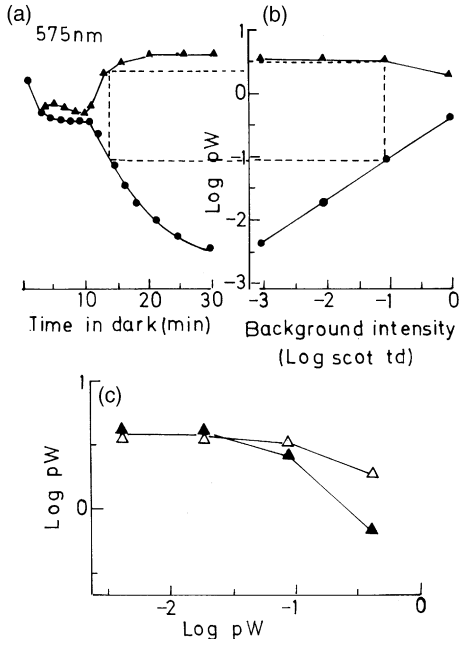

Fig. 3. Same as Fig. 1, except that the 575-nm test light was used. The stippled lines illustrate how the (c) sections were derived. Thus when, e.g., background intensity is −1 log scot td, the absolute threshold level is −1.05 log pW while the specific-nm threshold is 0.5 log pW. The same absolute-threshold level during dark adaptation, however, gives a specific-nm threshold of 0.38 log pW. This difference in specific-nm threshold level is shown in Fig. 3(c).

follows a negatively accelerated course during the last part of the dark-adaptation process.

It is well known that log difference between absolute threshold of dark-adapted rods and cones decreases when test wavelength is shifted from the short- and middle- to the long-wavelength region of the spectrum. Accordingly, the absolute rod threshold of the 620-nm

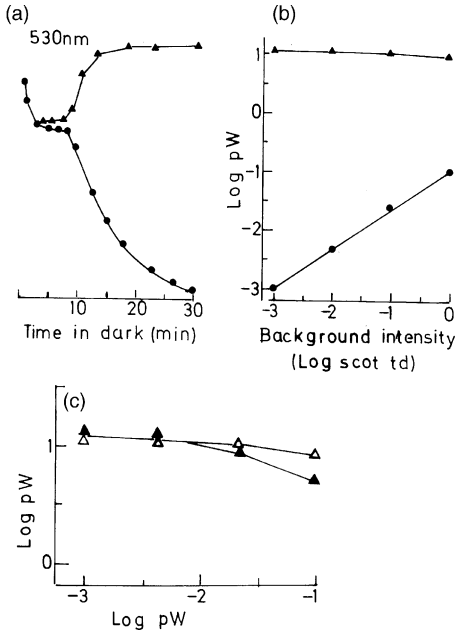

Fig. 4. Same as Fig. 1, except that the 530-nm test light was used.

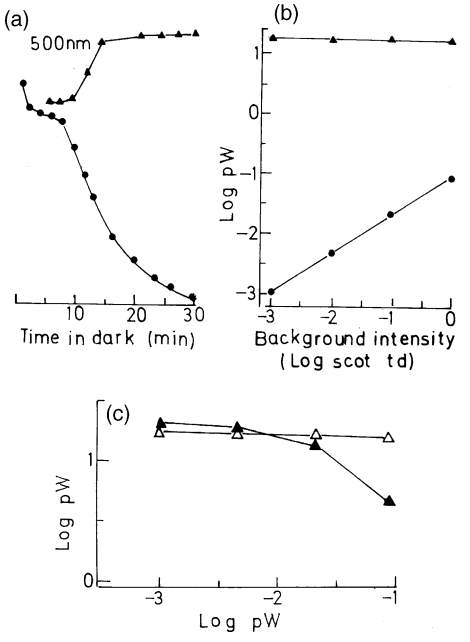

Fig. 5. Same as Fig. 1, except that the 500-nm test light was used.

test light falls only about 1-log unit below its cone-plateau level during the 30 min dark-adaptation period. Hence, during light adaptation (Fig. 1b), the absolute rod threshold of the 620-nm test light is suppressed above its cone-plateau level when the retinal illumination of the 7 deg scotopic background field is increased above the −2 log scot td level. Fortunately, by using the 500-nm test light, the change of the absolute rod threshold with rod light adaptation may be measured up to the highest scotopic background intensity level (0 log

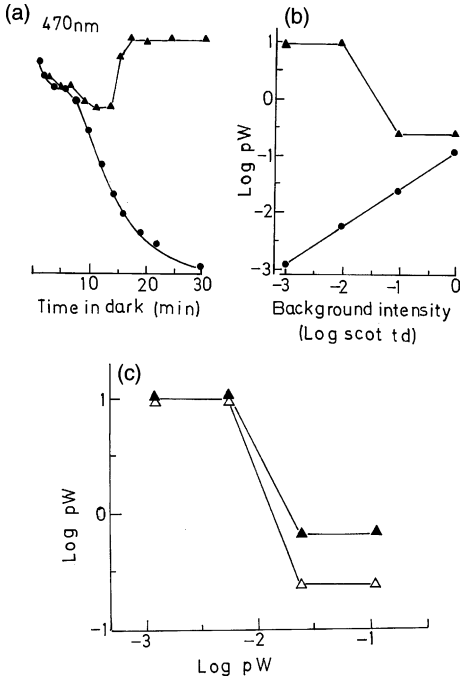

Fig. 6. Same as Fig. 1, except that the 470-nm test light was used.

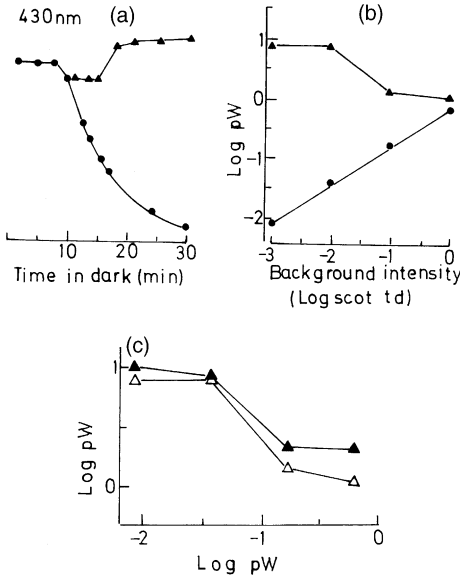

Fig. 7. Same as Fig. 1, except that the 430-nm test light was used.

scot td). This change of the absolute rod threshold obtained above the −2 log scot td level is represented in Fig. 1b by the data points on the stippled line. Similarly, the data points on the stippled line in Fig. 1a represent measurements of the absolute rod threshold obtained during the rod phase of dark adaptation when the 500-nm test light is used. As can be seen, from Fig. 1b, the absolute rod threshold with light adaptation follows an approximately linear slope of about 0.65, while the specific-hue threshold remains closely invariant up to −2 log scot td and then falls somewhat with increasing background intensity. The slope of 0.65 is identical to previous measurements of the t.v.i.-curve of a rod monochromat obtained under similar condition of experimentation (v. Sharpe, 1990, p. 70; Stabell, Nordby, & Stabell, 1987).

Fig. 1c shows specific-hue threshold levels for the dark and light adaptation of the rod receptor system when absolute rod thresholds are the same for the two conditions. (The stippled lines in Fig. 3a,b illustrate how the corresponding specific-hue threshold levels of dark and light adaptation were derived.) The results show that the specific-hue threshold, in general, is obtained at higher intensity levels for the light- as compared to the dark-adaptation condition.

The results obtained with the 600, 575, 530, and 500 nm test lights are similar to those obtained with the 620-nm test (see Figs. 2–5). However, log difference between the specific-hue thresholds obtained during rod dark and rod light adaptation is more pronounced with the 620-nm test (Figs. 1c–5c). Furthermore, the specific-hue threshold is seen to remain closely invariant with background intensity even up to the highest light adaptation level when the "green" test lights (530 and 500 nm) are used (Figs. 4b and 5b). Also it should be noted that the fall of absolute rod threshold subsequent to the cone–rod break increases markedly when the test wavelength changes from 620 to 500 nm. Despite this relative increase in rod activity, the total rise of the specific-hue threshold remains surprisingly similar (v. Figs. 1a–5a).

The results obtained with the "blue" test lights (470 and 430 nm) are markedly different from those at longer wavelengths (see Figs. 6 and 7). Thus it will be seen that the specific-hue threshold of blue obtained during dark adaptation falls somewhat subsequent to the cone–rod break (Figs. 6a and 7a). Moreover, as shown in Figs. 6c and 7c the specific-hue threshold obtained at the two highest background intensity levels is well *below* the specific-hue threshold level measured during the rod phase of dark adaptation. Furthermore, the hue observed with the 430-nm test light at the specific-hue threshold level appeared violet during the dark adaptation period, while it appeared purely blue under the light-adaptation condition.

Fig. 8 gives the specific-hue threshold of the 650-nm test light obtained during long-term dark adaptation under conditions where the test light was superimposed on the scotopic background field (Experiment III). The absolute and specific-hue thresholds of the isolated 650-nm test light obtained during long-term dark adaptation are also presented. It will be seen that the specific-hue threshold rises about 0.3-log unit when the scotopic background light is superimposed on the 650-nm test light during the cone-plateau period.

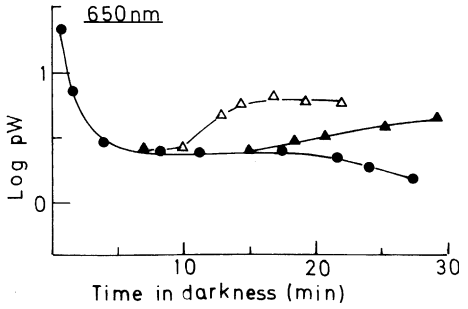

Fig. 8. Absolute (●) and specific-hue (▲) thresholds of the 650-nm test light obtained at 17 deg extrafoveally during long-term dark adaptation, together with the specific-hue threshold obtained when the 650-nm test light was superimposed on the scotopic 500-nm background light adaptation field (△). The intensity of the background light was 0.4-log unit below its cone-plateau level, i.e., −0.1 log scot td.

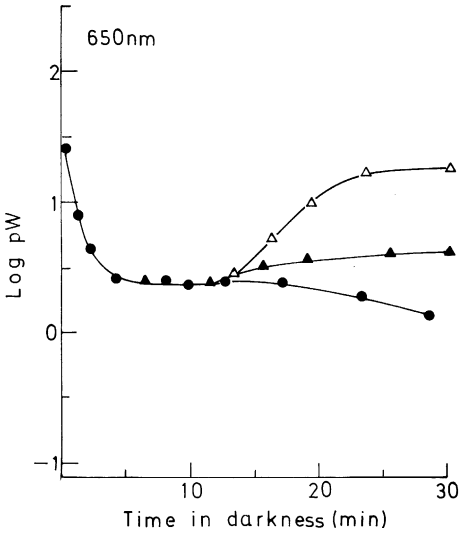

Fig. 9. Absolute (●) and specific-hue (▲) thresholds of the 650-nm test light at 17 deg extrafoveally measured during long-term dark adaptation, together with changes of specific-hue threshold (△) of a test light consisting of a mixture of the 650-nm light and a 500-nm scotopic light. The 500-nm scotopic light was set at a constant intensity level of 1.8-log unit below its cone-plateau level.

Fig. 9 shows the absolute- and specific-hue thresholds of the 650-nm test light obtained during long-term dark adaptation together with the specific-hue threshold of a test light consisting of a mixture of the 650-nm and a 500-nm scotopic light. The intensity of the 500-nm scotopic component was held constant at 1.8-log unit below its cone-plateau level while the intensity of the 650-nm light was increased in small steps until the specific-hue threshold was obtained (Experiment IV). The results show that the specific-hue threshold of the mixture light rises markedly during the last part of the dark-adaptation process.

Fig. 10 gives colour threshold of blue as a function of test wavelengths obtained when the eye is light adapted to a constant retinal illumination of −1 log scot td

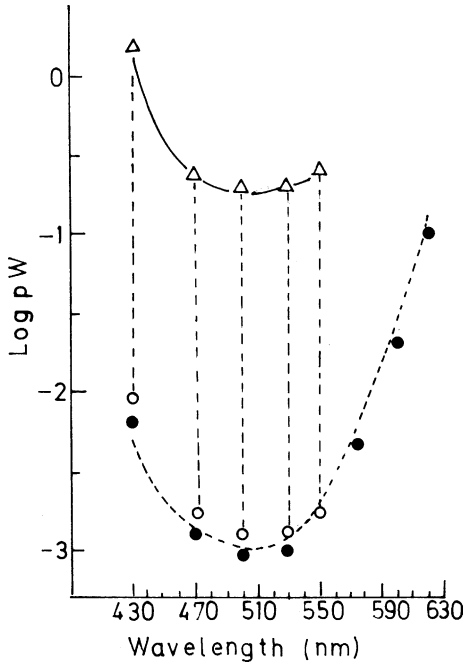

Fig. 10. Colour threshold of blue with rod light adaptation as a function of test wavelength (△). The retinal illumination of the background light was set at a constant level of −1 log scot td. For comparison, the data points have been displaced downwards (○) and shown together with absolute threshold of the different test wavelengths measured at 17 deg extrafoveally after 30 min dark adaptation (●) and the standard luminous efficiency function for scotopic vision (stippled curve).

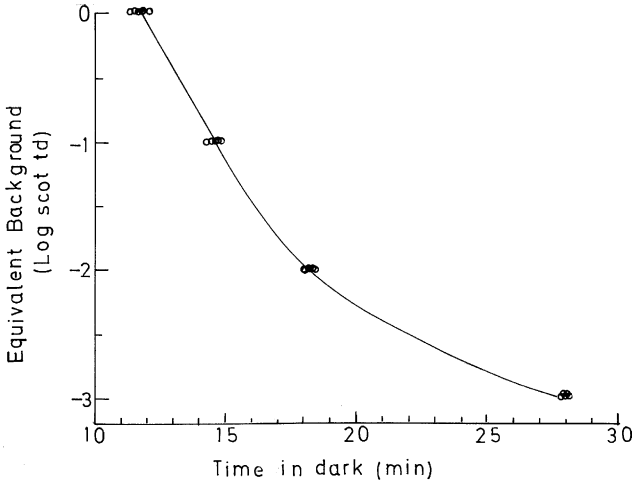

Fig. 11. The rod dark adaptation curves of the different test wavelengths (430, 470, 500, 530, 575, 600, and 620 nm) expressed as equivalent log background intensity plotted against time.

(Experiment V). For comparison, absolute thresholds of the different test wavelengths measured at 17 deg extrafoveally after 30 min dark adaptation are given (filled circles) as well as the standard relative spectral luminous efficiency function for scotopic vision (stippled curve). It

will be seen that the data points follow the scotopic curve closely.

In Fig. 11 the rod absolute dark-adaptation threshold curves for the seven different test wavelengths employed have been transformed into one of equivalent log background intensity against time (cf. Crawford, 1947). It is plain from the figure that the data points lie close to the same curve. Hence the equivalent background hypothesis appears to be valid for these scotopic absolute threshold measurements.

4. Discussion

The equivalence principle put forward by Stiles and Crawford (1932; Stiles, 1978, pp. 36–53) implies that when two different conditions of adaptation produce the same state of adaptation in a given retinal area, then any given test stimulus in this area will give identical results for the two conditions of adaptation. The present results (see Figs. 1c–7c) show that when absolute rod thresholds of the test lights are the same for the dark- and light-adaptation conditions, the specific-hue thresholds may be markedly different. Clearly, the two different conditions of adaptation do not produce the same state as defined by Stiles and Crawford (1932). Hence, the results invalidate our hypothesis that the change in specific-hue threshold with rod light and rod dark adaptation is controlled by the same mechanism.

The question then arises as to what factors may be involved in determining the differences obtained between the light and dark adaptation.

Previously, strong evidence has been presented suggesting that the rise of the specific-hue threshold during dark adaptation is determined by an increase of amount of rod signals activated by photic stimulation of rod receptors of the test area and not by rod signals from dark-adapted, unstimulated rods surrounding the test area (e.g., Alexander et al., 1988; Knight & Buck, 2001, 2002; Lie, 1963; Peachey, Seiple, Auerbach, & Armington, 1987, 1990; Stabell & Stabell, 1975, 1998, 2002). Accordingly, the rise has been explained on a colour-mixing hypothesis where the rod and cone systems activated by the test light contribute an achromatic and chromatic component respectively, and where the achromatic rod component increases during the rod phase of dark adaptation while the chromatic cone component stays constant (Lie, 1963; Spillmann & Conlon, 1972).

On this basis, the difference in specific-hue threshold level obtained between light and dark adaptation in the long-wave test region (Figs. 1–3) may most easily be explained on the suggestion that rod signals activated by the scotopic background light increase the desaturation effect (v. Stabell & Stabell, 2002).

In order to test this suggestion, the specific-hue threshold of a 650-nm test light was measured during the cone-plateau period under conditions where the test light was superimposed on a scotopic background light-adaptation field (see Experiment III). The results presented in Fig. 8 show that the specific-hue threshold of the photopic 650-nm test light rises about 0.3-log unit when the scotopic background light is added, confirming the suggestion.

Since the specific-hue threshold tends to fall markedly at the highest scotopic background intensities, however, the present results indicate that the effect of the increased rod activity excited by the background light is outweighed by the effect of the reduced rod activity excited by the test light when background light adaptation increases at these intensities. Furthermore, it should be noted that in addition to the desaturation effect generally obtained with rod intrusion at mesopic intensities, rod signals may also change the colour quality of mesopic test lights somewhat: toward yellow in the long-wave part of the spectrum and toward blue in the short-wave part (v. Buck, 2001; Buck, Knight, Fowler, & Hunt, 1998; Knight & Buck, 2001, 2002; Nerger, Volbrecht, Ayde, & Imhoff, 1998; Stabell & Stabell, 1975, 1979). Hence one might speculate that the yellow net rod influence in the long-wave region may be stronger with light adaptation compared to dark adaptation and thus contribute to the difference in specific-hue threshold obtained.

In contrast to the results obtained with long-wavelength tests, the specific-hue threshold of middle-wavelength tests (530 and 500 nm) was found to remain approximately invariant with scotopic background intensity (v. Figs. 4b and 5b). Thus, although absolute rod threshold is raised about two log units above its absolute dark-adapted level, there is no appreciable change in specific-hue threshold level. Similarly, it will be seen that the specific-hue threshold remains approximately invariant during the last part of the rod dark-adaptation process. Both these findings are in accord with previous evidence (e.g., Lie, 1963; Peachey et al., 1990; Prestrude et al., 1978; Spillmann & Conlon, 1972; Stabell & Stabell, 1965), but are not easily explained on the colour-mixing hypothesis of Lie (1963) and Spillmann and Conlon (1972). Clearly, one would expect the specific-hue threshold to change markedly.

The invariance of specific-hue threshold with change in absolute rod threshold obtained with the middle-wavelength tests both for the light- and dark-adaptation conditions might, however, be accounted for if one make the additional assumption that the most sensitive rod signals, which are generally assumed to be transferred mainly through the magnocellular system and to depend on summation of responses from a large number of neighbouring rod receptors, do not interact with, and therefore have no capacity to reduce the saturation of the test colour (see Stabell & Stabell, 1976, 1996).

In the present investigation we made a direct test of this interpretation (Experiment IV). Thus, absolute and

specific-hue thresholds were measured during long-term dark adaptation using a test light consisting of a mixture of a scotopic 500-nm light and a 650-nm light. The scotopic light was set at a constant intensity level of 1.8-log unit below its cone-plateau level while the intensity of the 650-nm light was increased to obtain the specific-hue threshold. The hypothesis was not confirmed. Thus, the results of the experiment presented in Fig. 9 clearly show that rod signals activated during the last part of the 500-nm rod dark-adaptation curve may affect the specific-hue threshold markedly. The question then arises why the most sensitive rod signals tend to elevate the specific-hue threshold when long- but not when short- and middle-wavelength test lights are employed.

The present results show that the specific-hue thresholds of the middle-wave tests start to rise at about the time when the rod receptor system during long-term dark adaptation first becomes excited by the test light, but then reaches a maximum long before the sensitivity of the rod system has reached the absolute dark-adapted threshold level. A possible explanation of this invariance of the specific-hue threshold during the last phase of rod dark adaptation is that the rod signals into colour-opponent pathways saturate when they increase above a certain level (v. Stabell & Stabell, 1996). However, it should be noted that both the time and the amount of rod signals activated by the test light necessary to reach the maximum level change with test wavelength (v. Figs. 1–7). Indeed, with the 650-nm deep red test light the maximum is not reached at all, apparently because too little rod activity is initiated. A test light consisting of a mixture of 650-nm and 500-nm lights may, on the other hand, activate the rod receptor system sufficiently, as evidenced by the results of Experiment IV (Fig. 9). The present results, however, do not provide any satisfactory answer as to why the rod impulses into the colour-opponent pathways saturate.

Previously, Spillmann and Conlon (1972) have measured both absolute and specific-hue thresholds during long-term dark adaptation and with increasing background field intensity, using a middle-wave test (a broadband 535-nm stimulus) centred 6 deg extrafoveally. In opposition to the present results they confirmed the equivalent background hypothesis. Thus they found that when absolute thresholds during dark and light adaptation were the same also the specific-hue thresholds were closely the same, i.e., the photochromatic intervals were closely the same.

Their results, however, cannot be taken as evidence in support of our equivalence hypothesis since (1) most of the elevation of the specific-hue threshold during the dark adaptation period was obtained before the cone–rod break, and (2) the major fall of the specific-hue threshold with light adaptation was obtained with background field luminance levels well above the cone-threshold level. Clearly, dark and light adaptation of the cone receptor systems may have influenced their measurements of absolute and specific-hue threshold levels and hence the size of the photochromatic intervals derived.

The results obtained with short-wavelength tests (470 and 430 nm) differ from those obtained with middle- and long-wavelength tests in two major respects. Firstly, the specific threshold of blue is seen to fall for a few minutes following the cone–rod break (v. Figs. 6a and 7a). Secondly, the colour threshold of blue was obtained at *lower* intensities under the light- as compared to the dark-adaptation condition at the highest light adaptation levels (Figs. 6c and 7c). These findings confirm our conclusion above that change in specific-hue threshold level with rod light and rod dark adaptation is not controlled by the same mechanism. Thus, on the one hand, well-founded evidence indicates that the fall in the specific threshold of blue during dark adaptation subsequent to the cone–rod break is due to a facilitation of the *chromatic cone response* by rod activity (v. Stabell & Stabell, 1971a, 1971b, 1976). In fact, at 3 and 6 deg extrafoveally a facilitation has been found for all colours of the spectrum when rod activity intrudes during long-term dark adaptation. Since the rod signals tend both to desaturate and facilitate cone-mediated colours simultaneously, however, facilitation is obtained, under the present condition of experimentation (17 deg extrafoveally) only for the saturated blue test colours.

The fall of the colour threshold of blue with light adaptation, on the other hand, is probably due to rod signals *per se* that are transmitted through colour-opponent pathways. This suggestion is in harmony with long-standing evidence that rod signals tend to prefer ''blue'' spectrally-opponent cells (v. Ambler, 1974; Ambler & Proctor, 1976; Buck, 1997, 2001; Knight & Buck, 2001, 2002; Stabell & Stabell, 1967, 1994). Accordingly, low threshold levels for blue with light adaptation were also found when green test lights (500, 530, and 550 nm) were employed. In fact, the spectral threshold curve for blue, adjusted along the ordinate scale, was found to coincide fairly well with the absolute spectral threshold curve of the rod system (v. Fig. 10).

The present investigation revives the century-old question as to whether light and dark adaptation of the rod-receptor system might be based on a common mechanism (Boll, 1877). Within the ''equivalent background'' tradition of Stiles and Crawford (1932) this question has been focused on whether similar biochemical processes regulate the desensitized states induced by sustained background light and by prior bleaching (see Barlow, 1964; Lamb, 1981; Pepperberg, 1984; Rushton, 1972; Stabell et al., 1987; Stiles, 1978, pp. 36–53). The model of equivalence presented by Barlow (1964) and later extended in an important paper by Lamb (1981) is well known. Both suggest that as far as detectability of a scotopic test light is concerned, the bleaching after-effect

is equivalent to the effect of a stabilised steady background of suitable intensity, and that the equivalent background during dark adaptation (the "noise" or "dark light") is caused by photon-like events in the rod outer segments. Thus, it is quite clear that their concept of equivalence is different from the classical equivalence concept put forward by Stiles and Crawford (1932).

However, on the assumption that the so-called "dark light" arises from photon-like events in the rod outer segments one might have expected the equivalence to hold under all test conditions (see Barlow, 1964, p. 54). Yet, Lamb (1981, p. 1781) carefully restricts his model to the detectability of test lights seen under scotopic conditions. It is obvious, then, that the present results do not invalidate this model. In order to test it, the background light-adaptation field would have to be properly stabilised and measurements would have to be restricted to absolute rod thresholds. Furthermore, both the temporal and spatial aspects of the "dark" and real lights would have to be identical.

The present results do show, however, that the rod–cone interaction mechanisms that determine the rise of the specific-hue threshold during the rod phase of long-term dark adaptation and its fall with rod light adaptation are different. Furthermore, the results show that signals from rods activated by the test light may facilitate chromatic-related cone responses during rod dark adaptation, while light adaptation of rods by a scotopic background light may produce a relative increase in blue-related responsiveness (i.e., a responsivity for blue-related activity of spectrally opponent cells) that may be triggered by rod signals.

In the present paper measurements have been restricted to absolute and specific-hue thresholds. Obviously, new important information as regards difference in rod–cone interaction processing between light and dark adaptation of the rod system may be revealed by measuring change in colour perception of test lights at mesopic intensities *above* the specific-hue threshold level (cf. Stabell & Stabell, 2002).

References

Alexander, K. R., Fishman, G. A., & Derlacki, D. J. (1988). Mechanisms of rod–cone interaction: Evidence from congenital stationary nightblindness. *Vision Research, 28*, 575–583.

Ambler, B. A. (1974). Hue discrimination in peripheral vision under conditions of dark and light adaptation. *Perception & Psychophysics, 15*, 586–590.

Ambler, B. A., & Proctor, R. W. (1976). Rod involvement in peripheral color processing. *Scandinavian Journal of Psychology, 17*, 142–148.

Barlow, H. B. (1964). Dark-adaptation: A new hypothesis. *Vision Research, 4*, 47–58.

Boll, F. (1877). Zur Anatomie und Physiologie der Retina. *Monatsberichte der Køniglich Preussischen Akademie der Wissenschaften*, pp. 783–787.

Buck, S. L. (1997). Influence of rod signals on hue perception: Evidence from successive scotopic contrast. *Vision Research, 37*, 1295–1301.

Buck, S. L. (2001). What is the hue of rod vision? *Color Research and Application, 26*(Suppl.), S57–S59.

Buck, S. L., Knight, R., Fowler, G., & Hunt, B. (1998). Rod influence on hue-scaling functions. *Vision Research, 38*, 3259–3263.

Crawford, C. B. (1947). Visual adaptation in relation to brief conditioning stimuli. *Proceedings of the Royal Society of London, Series B, 134*, 283–302.

Knight, R., & Buck, S. L. (2001). Rod influences on hue perception: Effect of background light level. *Color Research and Application, 26*(Suppl.), S60–S64.

Knight, R., & Buck, S. L. (2002). Time-dependent changes of rod influence on hue perception. *Vision Research, 42*, 1651–1662.

Lamb, T. D. (1981). The involvement of rod photoreceptors in dark adaptation. *Vision Research, 21*, 1773–1782.

Lie, I. (1963). Dark adaptation and the photochromatic interval. *Documenta Ophthalmologica, 17*, 411–510.

Loeser, L. (1904). Über den Einfluss der Dunkeladaptation auf die spezifische Farbenschwelle. *Zeitschrift für Psychologie und Physiologie der Sinnesorgane, 36*, 1–18.

Nerger, J. L., Volbrecht, V. J., Ayde, C. J., & Imhoff, S. M. (1998). Effect of the S-cone mosaic and rods on red/green equilibria. *Journal of the Optical Society of America A, 15*, 2816–2826.

Peachey, N. S., Seiple, W. H., Auerbach, E., & Armington, J. C. (1987). Rod influence on thresholds using different detection criteria during dark adaptation. *Acta Psychologica, 64*, 261–270.

Peachey, N. S., Alexander, K. R., & Derlacki, D. J. (1990). Spatial properties of rod–cone interactions in flicker and hue detection. *Vision Research, 30*, 1205–1210.

Pepperberg, D. R. (1984). Rhodopsin and visual adaptation: Analysis of photoreceptor threshold in the isolated skate retina. *Vision Research, 24*, 357–366.

Prestrude, A. M., Watkins, L., & Watkins, J. (1978). Interocular light adaptation effect on the Lie "specific threshold". *Vision Research, 18*, 855–857.

Reeves, A., Peachey, N. S., & Auerbach, E. (1986). Interocular sensitization to rod-detected test. *Vision Research, 26*, 1119–1127.

Rushton, W. A. H. (1972). Light and dark adaptation. *Investigative Ophthalmology, 11*, 503–517.

Schirillo, J. A., & Reeves, A. (2001). Color-naming of M-cone incremental flashes. *Color Research and Application, 26*, 132–140.

Sharpe, L. T. (1990). The light-adaptation of the human rod visual system. In R. F Hess, L. T. Sharpe, & K. Nordby (Eds.), *Night vision. Basic, clinical and applied aspects* (pp. 49–124). Cambridge: Cambridge University Press.

Spillmann, L., & Conlon, J. E. (1972). Photochromatic interval during dark adaptation and as a function of background luminance. *Journal of the Optical Society of America, 62*, 182–185.

Stabell, B., Nordby, K., & Stabell, U. (1987). Light-adaptation of the human rod system. *Clinical Vision Sciences, 2*, 83–91.

Stabell, U., & Stabell, B. (1965). Rods as color receptors. *Scandinavian Journal of Psychology, 6*, 195–200.

Stabell, B., & Stabell, U. (1967). Night vision as chromatic vision. *Scandinavian Journal of Psychology, 8*, 145–149.

Stabell, B., & Stabell, U. (1971a). Facilitation of chromatic cone activity by rod activity. I. Red-related cone activity. *Scandinavian Journal of Psychology, 12*, 99–105.

Stabell, U., & Stabell, B. (1971b). Facilitation of chromatic cone activity by rod activity. II. Variation of chromatic-related cone activity. *Scandinavian Journal of Psychology, 12*, 168–174.

Stabell, U., & Stabell, B. (1971c). Duration of scotopic contrast hues. *Scandinavian Journal of Psychology, 12*, 106–112.

Stabell, U., & Stabell, B. (1975). The effect of rod activity on colour matching functions. *Vision Research, 15*, 1119–1123.

Stabell, B., & Stabell, U. (1976). Effects of rod activity on color threshold. *Vision Research, 16*, 1105–1110.

Stabell, B., & Stabell, U. (1979). Rod and cone contributions to change in hue with eccentricity. *Vision Research, 19*, 1121–1125.

Stabell, U., & Stabell, B. (1994). Mechanisms of chromatic rod vision in scotopic illumination. *Vision Research, 34*, 1019–1027.

Stabell, B., & Stabell, U. (1996). Peripheral colour vision: Effects of rod intrusion at different eccentricities. *Vision Research, 36*, 3407–3414.

Stabell, B., & Stabell, U. (1998). Chromatic rod–cone interaction during dark adaptation. *Journal of the Optical Society of America A, 15*, 2809–2815.

Stabell, B., & Stabell, U. (2002). Effects of rod activity on color perception with light adaptation. *Journal of the Optical Society of America A, 19*, 1249–1258.

Stiles, W. S. (1978). *Mechanisms of colour vision. Selected papers of W.S. Stiles F.R.S., with a new introductory essay* (pp. 36–53). London: Academic Press.

Stiles, W. S. & Crawford, B. A. (1932). *Equivalent adaptation levels in localized retinal areas*. Report of a joint discussion on vision held on June 3, 1932 at the Imperial College of Science by the Physical and Optical Societies. London: Cambridge University Press.

Wright, W. D. (1946). *Researches on normal and defective colour vision*. London: (Henry) Kimpton.